

Towards a Complete Synthetic Theory of Evolution

by

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COMPLETE
TOWARDS A ~~NEW~~ SYNTHETIC THEORY OF EVOLUTION

THE CONTROVERSY

Looking through the issues of American Biology Teacher Magazine for the years 1970 to 1973 one finds a preponderance of articles debating the pros and cons of Special Creation as opposed to Evolution. This was sparked by the attempt of the Creation Research Society, headed by Dwaine T. Gish, to have Special Creation taught in high schools, along with Evolution, as a valid alternative. Their stand is reviewed by Aulie (American Biology Teacher, 1972) but the important controversy derives from other articles and letters by Gish (1970,71), Salisbury (1971), Moore (1973) and from evolutionists Stebbins (1973), Dobzhansky (1973), Mayr (1971), Robinson (1971) and Hardin (1973).

One basis for dispute is statistical probability. Salisbury worries whether new useful genes could have accumulated by random appearance. He points out that the number of amino acid sequences possible (and therefore nucleic acid sequences) is so much larger than the ones that could or have been used that the probability of getting them by chance is extremely small. Gish refers to similar arguments by Eden and others in Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution, (1967), a symposium of mathematicians and biologists at the Wistar Institute.

This view is challenged by Smith (1969) and by others at the Wistar Symposium on the basis that acquisition of new features is not random but determined and directed by pre-existing form. Indeed such acquisitive evolution has been shown to occur in bacteria by Lin et al (1976) and Eden himself, during the symposium, recognized the inadequacy of mathematical calculations, saying, in reference to Mayr's talk, "I

welcome the fact that he has turned the theme of the meeting upside down and suggested that there are evolutionary challenges to mathematics. That, precisely, is the point."

Stebbins (ABTM, 1973, pages 1, 60) comments that "The oft repeated statement that, because mutations are random relative to the adaptive demands of the environment, therefore evolution depends upon chance, is a dangerous bit of false logic" and that "In all instances the built-in order and design that already exists exercises a dominant influence over the direction of further evolution." The truth and importance of this statement should be apparent by the end of this paper.

Gish's argument comes mainly from an interpretation of the fossil record. One problem is the well known sudden appearance of each distinctly separate invertebrate phylum at the beginning of the Cambrian. As well, he points out the systematic lack of transitional forms throughout the entire record. He says that the number of transitional forms predicted by the evolution theory is inconceivably great and that "it seems clear, then, that after 150 years of intense searching, a very large number of obvious transitional forms would have been discovered if the predictions of evolution theory are valid." (Gish, p. 36).

But, he finds, there are tremendous gaps, as found between the crossopterygian fish and the labyrinthodont amphibia, the appearance of flying animals at independant times with no lead-up, and the amphibian/reptile and reptile/mammal transitions where, he says, the gradual change indicated by bones is irrelevant because the real change was in the soft parts and must have involved dramatic revolution.

There are also problems such as how an organism, during the evolution

of the middle ear, "would hear while dragging two of its jaw bones up into its ear." (Gish, p. 138)

He stresses, too, the problem first discussed by Goldschmidt (1952) and Simpson (1949) that, "when a new phylum, class, or order appears, there follows a quick, explosive (in terms of geological time) diversification so that practically all orders or families known appear suddenly and without any apparent transitions." (Goldschmidt, 1952)

In Kuhn's interpretation of this evidence, (1942) "The fact of descent remains. However, descent beyond the typologically circumscribed boundaries is nowhere demonstrable. Therefore, we can indeed speak about a descent within the types but not about a descent of types." The Creationists maintain, then, that the variation that has occurred since creation has been restricted within the limits of each created kind.

Stebbins (ABT, 1973, p. 60) disagrees with this interpretation of the record:

"In short, both the presence and the abundance of certain transitional forms, as well as the complete absence of other transitional forms, are best interpreted as the result of highly irregular and fortuitous preservation of fossils. The gaps in the record are much more closely related to the abundance, size, presence of hard parts, and nature of life of the forms concerned than to their position as transitional forms rather than typical members of modern groups. Fossils do not provide us with a complete record of the evolution of living organisms. Nevertheless, they do provide evidence of transitions between major groups often enough for us to be reasonably confident that these groups evolved gradually one from the other or that both evolved from an extinct common ancestor."

He singles out the examples of coelocanth fishes and Sphenodon reptiles whose fossils stop appearing ^{cut} over 100 million years ago, but nevertheless are alive today.

Dobzhansky (ABT, 1973) points to the exquisite adaptiveness and diversity of organisms as found in the study of comparative anatomy and embryology as evidence of evolution: "Was the Creator in a jocular mood when he made *Psilopa petrolei* for California oil-fields and species of *Drosophila* to live exclusively on some body-parts of certain land crabs on only certain islands in the Caribbean? The organic diversity becomes, however, reasonable and understandable if the Creator has created the living world not by caprice but by evolution propelled by natural selection." (p. 127)

Mayr (ABT, 1971) says that most evolutionary change may occur only in small populations, thereby leaving few intermediates. In addition, he argues that showing problems with evolutionary theory does not prove Special Creation, nor can Gish find anything that actually falsifies evolution.

The theory of evolution may be unfalsifiable, and this would disqualify it as a formal theory. Although there is reasonable controversy about whether evolution is actually a "scientific theory" (as seen by the arguments of Gish, 1970, 1973 and Moore, 1973 versus those referred to by Robinson, 1971) there is little reasonable doubt as to the status of Special Creation: Hardin (ABT, 1973) refers to it as a "rejection of rationality."

Obviously, as Dobzhansky (ABT, 1973) points out, the fossils are old and there has been an overall progression. "However offensive the notion may be to religious feelings and to reason, the anti-~~evolutionists~~ must ...accuse the Creator of cheating. They must insist that he deliberately

arranged things exactly as if this method of creation was evolution, intentionally to mislead sincere seekers of truth." (p. 129)

In short, there is no need to resort to creationist explanations. The fact of evolution is obvious. But it is also apparent that there is a definite problem in explaining to any degree of satisfaction just how evolution has occurred.

Part of the controversy is this confusion of the fact of evolution with the mechanism. From Dobzhansky (ABT, p. 129):

"Disagreements and clashes of opinion are rife among biologists, as they should be in a living and growing science. Anti-evolutionists mistake, or pretend to mistake, these disagreements as indications of dubiousness of the entire doctrine of evolution. Let me try to make crystal clear what is established beyond reasonable doubt, and what needs further study, about evolution. Evolution as a process that has always gone on in the history of the earth can be doubted only by those who are ignorant of the evidence or are resistant to evidence, owing to emotional blocks or to plain bigotry. By contrast, the mechanisms that bring evolution about certainly need study and clarification. There are no alternatives to evolution as history that can withstand critical examination. Yet we are constantly learning new and important facts about evolutionary mechanisms."

SPECIAL AND GENERAL EVOLUTION

Living organisms can be observed over the course of time to undergo changes that may lead to the formation of new species. This is what Kerkut calls the "Special Theory of Evolution". It embodies the Neo-Darwinian theory developed by Haldane, Fisher and Wright. On the other hand there is the theory that all living forms arose progressively from a common source. This, Kerkut calls the "General Theory of Evolution". Nobody questions the importance of Neo-Darwinian theory for intraspecific and interspecific evolution: "on this point corroboration obtains to a degree that is rare in biology, and which surely makes Neo-Darwinism one of the most successful biological theories". (Lovtrup, p. 396) It is well supported by observations of animal breeding, Kettlewell's (1973) classic pepper-moth study, the examples mentioned by Hardin (ABT, 1973), observations of allopatric population and species variations, and so on.

But this principle has been extrapolated, unmodified, to explain the general theory, and here it runs into the problems cited by creationists. "Extrapolation is an acknowledged scientific expedient which often leads to right answers, but it is a dangerous approach unless it is employed with discrimination." (Lovtrup, 1974, p. 396). Moore (ABT, 1973) has used this as a criticism of evolution - that proof of the special theory is used as proof of the general.

Here is the use of the creationists' contentions: they force us to re-evaluate our theory. The problem has also been recognized by many biologists, notably embryologists and morphologists such as Waddington, Lovtrup, Frazetta and Sinnott, and by non-biologists such as Whyte and

Koestler. They have suggested other factors to include for a complete causal theory, and it is chiefly from their work that I will draw my argument. These authors are unequivocal and unanimous in their criticism of the synthetic theory:

"Incessant repetition of this unproved claim, glossing lightly over the difficulties, and the assumption of an arrogant attitude toward those who are not so easily swayed by fashions in science, are considered to afford scientific proof of the doctrine." (Goldschmidt, 1952, p. 94).

"An independent mind may question whether too grand and comprehensive a theory claiming to cover distant past history has not been built on relatively thin evidence, however attractive and powerful its ideas." (Whyte, 1965, p. 74).

"Perhaps such a simplification was justified when it was a question of establishing the relevance of Mendelian genetics to evolutionary theory, but it can only lead to an impoverishment of our ideas if we are not willing to go further, now that it has served its turn." (Waddington, 1974, p. 58).

Mayr, though one of the prominent Neo-Darwinists, stated at the Wistar Symposium (1967, p. 54) that "Evolution, again and again, has resulted in unique phenomena and in startlingly unpredictable phenomena. If we set up our programs in too deterministic a manner, I am afraid we will never be able to arrive at a realistic interpretation of evolution."

From Whyte again (1965, p. 30): "It would have been wiser to claim that the theory described one major mechanism of evolution, but that there was no evidence that it was the only one. The synthetic theory

was a necessary but not a sufficient theory of the directive factors in evolution. However, nearly all the leading exponents of the theory presented it as absolute: adaptive selection, substantially as outlined by Darwin, was the mechanism by which adaptively undirected mutations resulted in the progressive evolution of living forms."

In fact, Darwin himself assumed his theory to be one, not the only, factor in the cause of evolution. I would like to now look at the other factors that have been neglected.

PROPOSAL

Let us assume that the discontinuity of the fossil record indicates a fundamental aspect of evolution: that many transitions were not recorded because they did not exist: that these changes involved not gradual transition but sudden leaps in evolution.

This, then, is the most significant factor for a new theory of evolutionary causation to deal with. The solution could provide Man with a more solid grasp of his existential position, for to quote Waddington (1974, p. vii): "It is where it comes into conflict with the Theory of Intelligent Design that the Theory of Evolution becomes something of general human importance, rather than a mere piece of technical specialized expertise; and it is just in these areas of conflict that the Neo-Darwinist paradigm is misleading. The successes of Neo-Darwinism... will be largely beside the point when we are considering Evolution as a relatively new, major component of man's thinking about his place in the universe."

The present Synthetic Theory of Evolution is a combination of Darwinian natural selection, mendelian and quantitative genetics, and statistical mathematics. I propose that by the addition to this of knowledge of the development of organisms (epigenetics), a solution will be found. Here we will find the means by which organisms can, and have, changed non-randomly, and often radically, so that, "... whereas the import of the previous evolutionary theories can be sloganized in Jacques Monod's phrase 'Chance and Necessity', the fourth paradigm would substitute slogans such as 'Learning and Innovation', or 'Adapting and Improvising', or, if you like a more with-it jargon, 'Recompiling and Heuristic Search'." (Waddington, 1974, p. vi).

In the remainder of this essay I intend to show that:

- 1) evolution, according to paleontology, has involved many radical and sudden transitions to new "archetypal strategies";
- 2) that even according to the Neo-Darwinian theory many of the hypothesized transitional forms could not have existed;
- 3) that the adaptability inherent (and selected for) in the developmental processes of living beings allows for, and in a sense directs, these radical changes; and
- 4) that the kind of selection involved in the survival of these new types may be quite different from that implied by the Neo-Darwinian model.

THE PROBLEM

Let us look more closely at what we are trying to explain.

The primary problem is the tendency toward systematic discontinuity in the record of Life's history. (Frazetta, 1975 - see figure 1.)

Most striking is the fact that all fossilizable metazoan phyla appear in the Cambrian ~~except for the chordata which appear shortly after in the Ordovician~~. No new animals with an organization unique enough to be classed as a new phylum have evolved in the following one-half billion years.

By the end of the Paleozoic era the appearance of new classes has all but stopped. Two more classes appear in the next two periods - the mammals and birds. Thus novel organizations distinct enough to constitute new classes did not develop in the last 135 million years or so.

Orders follow a similar deceleration. For example, of the 50 or so aquatic orders almost all appear in the Lower Paleozoic, then three more in the Middle Paleozoic and finally four more during the Mesozoic, but then, in the Cenozoic, there is a burst of new ones, the placentals. After the Eocene there are no new chordate orders.

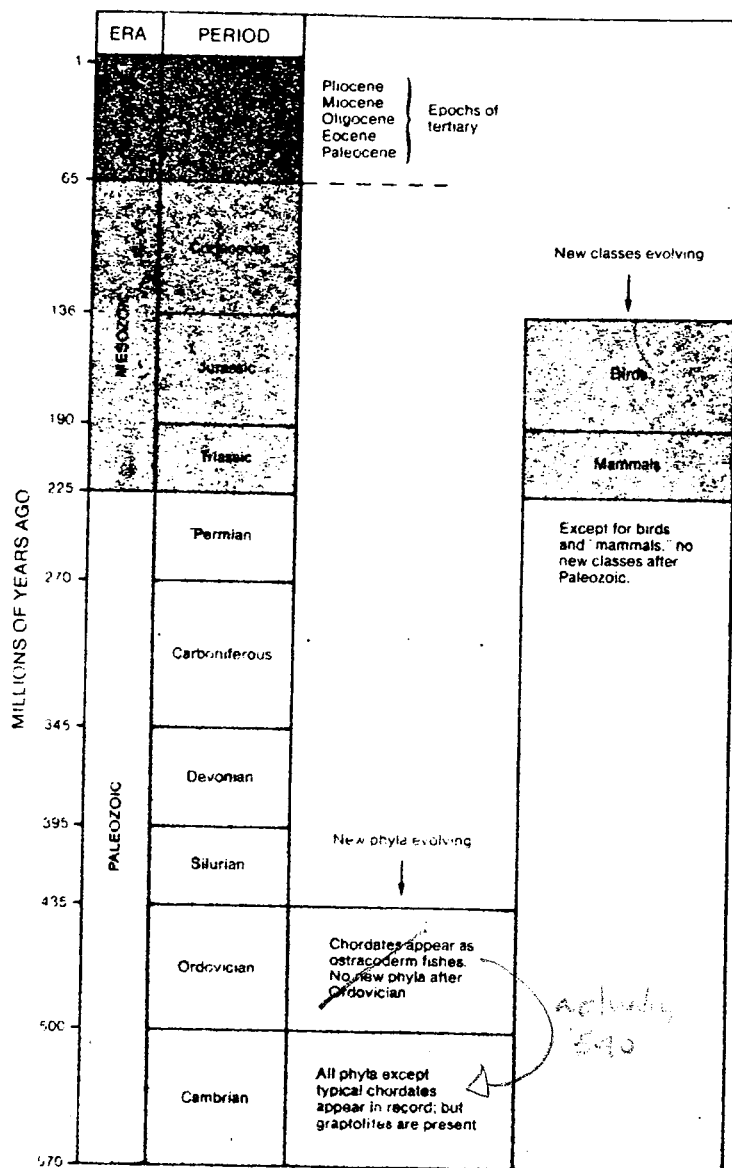


Figure 1.

Evolution appears to have been more "rapid" in the past, in terms of large scale innovation, slowing down in recent times to relatively trivial changes. As well, it seems that sometimes there have been sudden surges in the appearances of many new distinct groups. No correlation with major environmental change has been found.

"As we descend to lower taxonomic levels, from phyla to classes, to orders, and so on, we are further enveloped by this curious matter. Major evolutionary events seem to have occurred long ago, with fewer such events as recent days are approached." (Frazetta, 1975, p. 58).

To state this most clearly: evolution seems often to have proceeded from higher to lower taxonomic rank, rather than the reverse, as is held by Neo-Darwinists. Fig. 2 shows a very simple phyletic hierarchy. Try and imagine it developing through time from the bottom up, so that "the accumulation of the changes of the speciation mode tends towards segregations of higher category." (Simpson, 1944, p. 202).

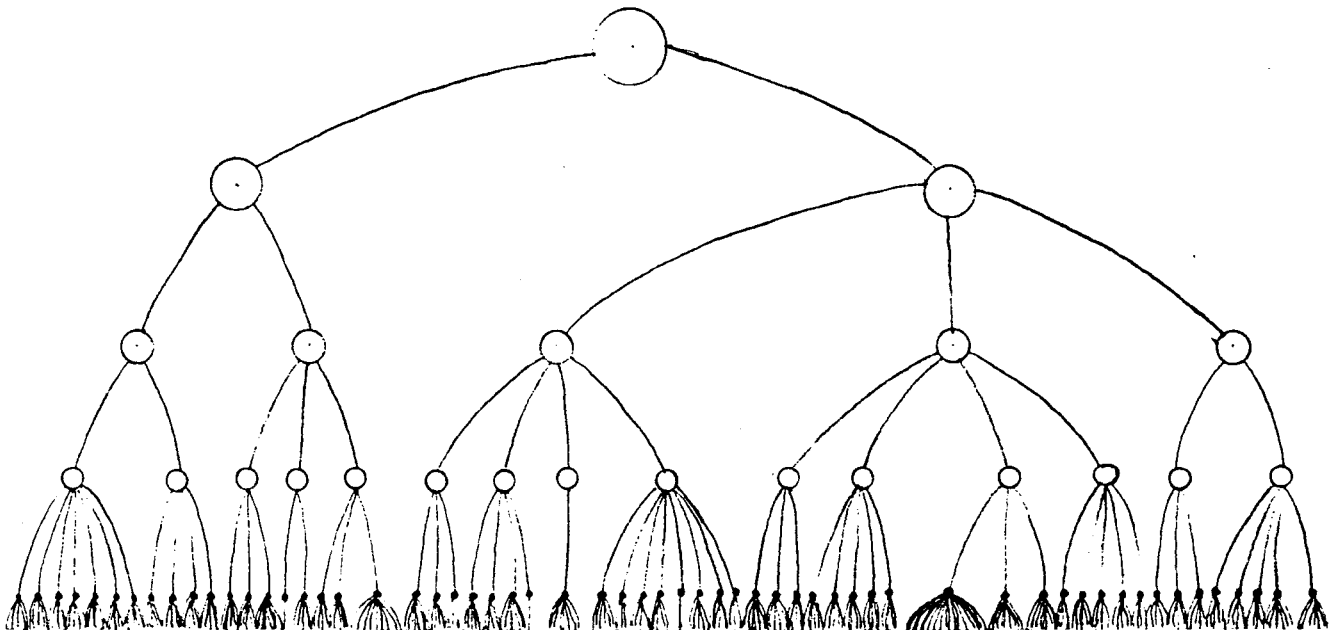


figure 2.

Indeed, one finds it virtually impossible to see how such groupings could develop from gradual divergence of species.

Lovtrup (1974, pp. 484, 485) says:

"The question of the direction of evolution has, as a matter of undisputable fact, been settled...: phylogenetic evolution has proceeded from the apex to to the base of the systematic hierarchies...Evolution involving divergence on the species level must result in chaos rather than system in the organic world...even a very superficial consideration of the nature of intraspecific and interspecific variations shows that they seldom are of the same kind as those distinguishing taxa of higher - or superior - rank. It is evidently impossible to justify the view that the 'individual', subspecific and specific variations known to occur within the classes Aves and Reptilia could ever, through accumulation, be concerned with origination of such features as feathers, wings or beak. Likewise, the outstanding distinction between Chordata and Invertebrata, the formation of a notochord at an early stage of development, surely is an all-or-none phenomenon, arising through one specific epigenetic mechanism. As has been brought out above, the main phyletic character is the unique archetypical body plan, whereas the distinguishing marks of the successive taxa of lower rank consist of a gradual series of less and less comprehensive modifications of this body plan, ending with the specific characters which usually are minor changes in form, size and pattern...."

Waddington (1975) pinpoints the problem, saying, "We certainly cannot be content without some further understanding of how these small-scale processes of natural selection of minor variants in relation to immediate needs have produced a restricted number of basic 'archetypes' - the protozoan, the annelid, the insect, the vertebrate - which are flexible enough to become adapted to almost any system of life yet have sufficient inherent stability to do so without losing their essential character." (p. 230)

A second problem for the new theory to deal with derives directly from the implications of the Neo-Darwinian theory. It is generally held that phenotypic differences are always small; organisms are at an adaptive "peak", so that any great or sudden alteration in phenotype will disrupt their stable position. Thus it is thought that large scale variants will be selected out and only lesser ones will be tolerated. This implies that evolution proceeds in small steps, and builds gradually.

This view leads to certain contradictions (which the Neo-Darwinists have somehow managed to ignore). For one, certain properties could not have originated through accumulation. Changes in the number of segments, appendages, digits or heart chambers obviously require large all-or-none changes. Likewise it is generally accepted that the transition from procaryotes to eucaryotes was essentially instantaneous, as proposed by the endosymbiotic theory. (Sagan, 1967, Margulis, 1970)

Secondly, even in many cases where the gradual origination of a property is possible, "it is unwarranted to invoke natural selection before the new function has been assumed. Thus, the small bud that would represent an incipient limb, rather than a benefit, might be a nuisance against which the selective forces would act." (Lovtrup, 1974, p. 436).

From Lovtrup again (1974, p. 488): "There certainly must have been many more transitional forms between reptiles and birds than the few ones known to us. This does not, however, allow for the conclusion that transitions between systematics have proceeded in infinitesimal steps. This alternative cannot but give rise to 'hopeless monsters'. As such I

would consider a reptile with 117/300 of the forelimbs being feet and the remainder wings, or a gastropod turned 209/300 into a cephalopod. If these animals are the ones the Neo-Darwinian evolutionists are so anxiously hoping to find in the fossil record, then I am sure that Goldschmidt (1940) and Schindewolf (1950) are correct when they contend that this expectation will never be fulfilled. Such animals never did and never could exist, for their formation would be a morphological, their survival an ecological, impossibility."

A good illustration of this is the transition from the amphibian aquatic to the reptilian terrestrial egg. Such an adaptation involves the acquisition of a tough shell to conserve water, an allantois to store poisonous wastes, a means of getting out of the shell, and a larger yolk and albumen. If any one of these factors is missing the result is fatal. On this Koestler remarks (1967, p. 129), "Each change, taken in isolation, would be harmful, and work against survival. You cannot have a mutation A occurring alone, preserve it by natural selection, and then wait a few thousand or million years until mutation B joins it, and so on, to C and D. Each mutation occurring alone would be wiped out before it could be combined with the others. They are all interdependent. The doctrine that their coming together was due to a series of blind coincidences is an affront not only to commonsense but to the basic principles of scientific explanation."

In summary, a complete theory of evolution must account for the "descent within types only" (as the Creationists call it) that is implied by the "downward" origination of taxonomic groups we have seen; and this goes hand-in-hand with the inconsistency apparent in the strict Neo-Darwinian explanation of transition between major types.

WHERE TO LOOK

The bulk of evolution has involved a large increase in DNA, but relatively little increase in protein diversity. In fact, as Medawar (1967, p. 8) stated: "In a certain important sense all chemical evolution in living organisms stopped millions of years before even our faintest and most distant records of life began. So far as I know, no new kind of chemical compound has come into being over a period of evolution that began long before animals became differentiated from plants....I have no views on the processes of evolution that brought new kinds of chemical compounds into existence, but I should not be surprised to find them very different from the forms of evolution that have been in progress since".

Indeed, what has been in progress since has been, not an increase in structural genes coding for proteins, but an increase in regulator genes, which determine the degree of integrated cellular activity.

(Dobzhansky, 1970, Stebbins, 1969, Britten & Davidson, 1969)

At a given locus in a eucaryote chromosome only 1/10 to 1/20 of the DNA is needed to code for an average protein - the rest must be regulatory in nature. Insufficient emphasis is given to this fact in schools. Though we know virtually nothing about the functioning of all these regulator genes, I feel that it must be, at this time, the single most important aspect of eucaryotes to study for an understanding of their organization and evolution.

Even professional geneticists misplace their emphasis. For instance, Clarke (1975) dealing with protein polymorphism in Scientific American,

stated, most probably at a careless moment, that "evolution largely consists in the progressive substitution of one amino-acid for another." This is unequivocally false.

The chief function of regulatory activity is the determination of the appearance of the structural gene products in time and space - that is: form.

Sinnott (1963) stresses the significance of form. "Biologists", he says, "are coming to realize that not simply metabolic changes, nor growth processes, nor gene action, nor the biochemical basis of living stuff provide the central problem of their science, but the way in which these phenomena are so interrelated that a formed organism is produced." (p. 8).

Furthermore:

"Substance, on one hand and form on the other are the two chief attributes of the objects that confront us daily and especially of those incredibly complex units that we call organisms. The problem cuts deeply through our attitudes and our philosophies. Substance-minded people are impressed with the stuff of which things are made. They tend to be practical, hard-headed, and materialistic. Form-minded ones, on the contrary, look chiefly at the patterns and relationships of things. Since all the arts are concerned with form, in one aspect or another, people's outlook on the world is affected by this difference in attitude. This is a very ancient antithesis and has been stated in many ways. Today it is expressed vividly in the problem of translating a very remarkable substance, deoxy-ribonucleic acid, into the form of an organism. There is no place here for an easy dogmatism or philosophical naiveté." (p. 15).

The problem of multicellular evolution is essentially a form problem. Ontogeny is the process whereby organic forms come into being,

and "not only are ontogeny and phylogeny in many respects related but ontogeny is theoretically primary." (Whyte, 1965, p. 42)

Thus Lovtrup (1974, p. 496) says that "Phylogenesis is the outcome of successive changes in the process of ontogenesis, and we therefore cannot hope ever to understand how genes may accomplish the former phenomenon unless we know how they carry out the latter. It is for this reason that the study of epigenesis is so important also for the theory of evolution."

With this in mind, let us look at what is involved in changing the form of living organisms.

INTEGRATION, CORRELATION AND ADAPTABILITY

"The concepts derived from the study of characteristics treated individually are customarily extended to explain all evolutionary phenomena. Too often the extension is made with a vague confidence that what is true for simple, isolated characters must be equally and also sufficiently true for sets of interrelated features. I am suspicious, however, that an understanding of evolution taken from consideration of individual characters might be a bit different from an understanding of the evolution of complex, integrated systems." (Frazetta, 1975, p.3)

An organism is not an aggregate of "unit" traits or characters. These concepts are merely abstractions devised for communicating observations. Dobzhansky (1970) gives numerous examples of "pleiotropic" effects, where, for example, the mutant "vestigial", referring to reduced wing size in *Drosophila*, also changes the balances, the orientation of certain bristles, the wing muscles, the spermatheca shape, developmental rate, fecundity and viability.

He cautions that "talking about traits as though they were independent entities is responsible for much confusion in biological, and particularly in evolutionary, thought."

Frazetta (1975) emphasizes that the complex adaptations of organisms can be thought of as analogous to a machine where the performance depends upon exact cooperation among its parts. No part can be altered without changing the functioning of the entire machine. He discusses the Peaucellier straight line mechanism (fig. 3) to illustrate this point.

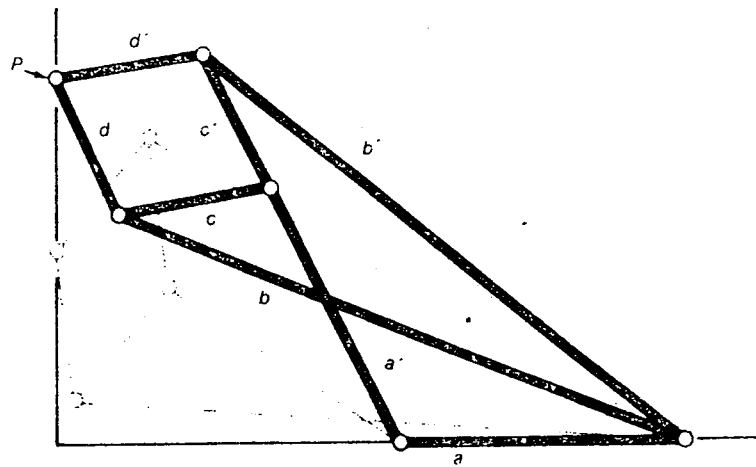


Fig. 3. Peaucellier straight-line mechanism. The grey image shows the mechanism in a displaced position. The point P always traces a straight line along the ordinate axis.

Here the point P must always move in a straight line for the proper functioning of the machine. In order to shift the trajectory of P to one side there must be a simultaneous change in the lengths of each element, in accordance with specific rules of proportion.

Likewise the acquisition of an altered biological adaptation would require the same sort of integration. In fact, organisms are capable of this:

"The difficulty largely disappears if one remembers that an organ like an eye is not simply a collection of elements, such as a retina, a lens, an iris, and so on, which are put together and happen to fit. It is something which is gradually formed while the adult animal is developing out of the egg; and as the eye forms, the different parts influence one another. Several people have shown that if, by some experimental means the retina and eyeball are made larger than usual, that in itself will cause a larger lens to appear, of at least approximately the appropriate size for vision. There is no reason, therefore, why a chance mutation should not affect the whole organ in a harmonious way; and there is a reasonable possibility that it might improve it....A random change in a hereditary factor will, in fact, not usually result in an alteration in just one element of the adult animal; it will bring about a shift in the whole developmental system, and may thus alter a complex organ as a whole." (Waddington, 1975, p. 52).

Frazetta discusses examples of integrated change in evolution.

One comes from the work of Hampé, 1959, on the differences in hind-leg structure between modern birds and Archaeopteryx, fig. 4. By allowing the normally reduced fibula of a chick to have access to a larger supply of cells during embryonic development it was able to grow to full length as in Archaeopteryx. As well, the ankle bones, normally fused to the tibia, remained separate.

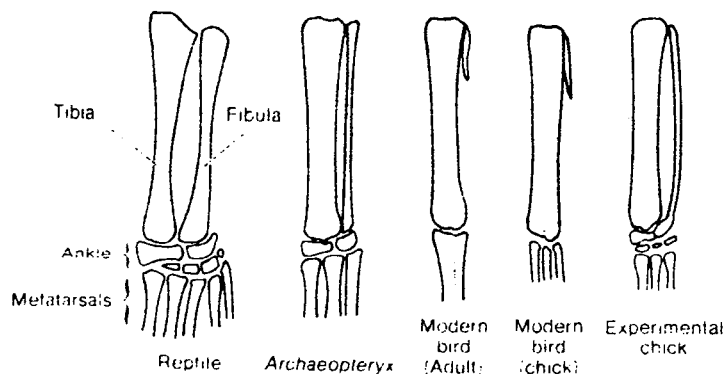
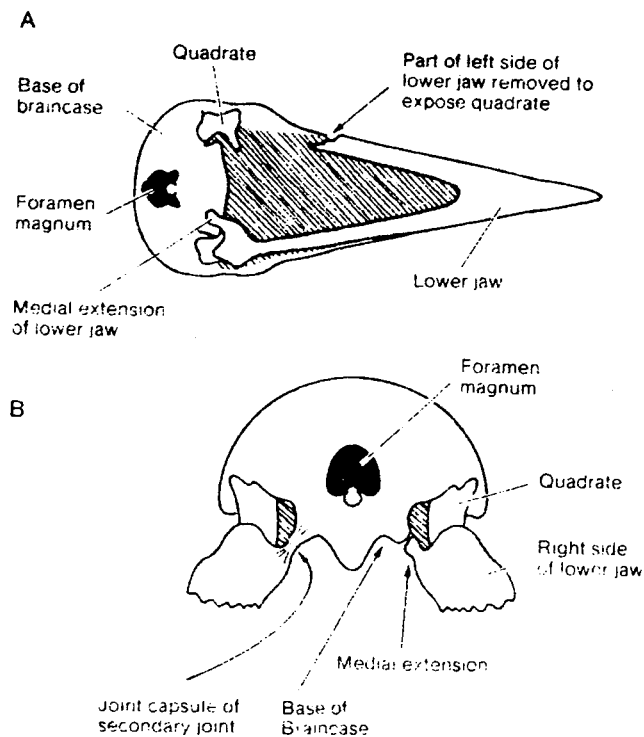


Figure 4.

So the difference between Archaeopteryx and modern birds could have been a minor genetic mutation that restricted the amount of material available to the fibula. This then automatically influenced the factors controlling ankle development, and resulted in a new functional arrangement.

A second example is noted by Bock (1959) regarding certain birds which have an "extra" joint in their jaws, a "medial brace", which lends greater strength, as their feeding habits require. See figure 5. Primitive birds do not have this joint, and it has arisen independently several times.



A. Ventral and B. posterior views of a bird skull possessing a secondary jaw joint. (Modified from Bock, 1959.)

Figure 5.

The adaptation may have arisen due to selection for stronger jaw musculature, which would require enlargement of the medial extension. When brought close to the braincase an extra joint could be selected for. Frazetta (1975) discusses this adaptation:(pp. 98-89)

"In some ways the secondary jaw joint is a major, evolutionary novelty; in some others it is not. Already present in the evolving birds was the capacity of bones and their associated musculature to adjust to one another. And the formation of the medial joint itself could have arisen quite easily, for, as Bock points out, bones and their surrounding tissues possess the ability to fashion a complexly structured movable joint (termed a pseudoarthrosis) where two bony elements are brought into moving contact. Considering these facts it could be said that the secondary joint, though an evolutionary novelty, did not require a very major change in the morphogenetic foundation of the organism. The major adaptive feature involved was the bone-muscle system, whose capacity for complex interaction permitted the evolution of the medial bracing device, but which had already evolved before birds appeared on earth."

A third example comes from Waddington (1962). He shows that a mutant gene in drosophila can move the developing limb-buds closer together. They then interact to produce a common appendage reminiscent of a labium. Such a complex alteration as this then, can occur by the influence of one simple mutation, rather than selection of many small changes that gradually tend to form a labium structure.

There is another kind of co-ordinated regulation which I will call "correlation", as opposed to "integration". This is a convenience for presentation, for the two can hardly be separated. Correlation becomes apparent when studying growth (Sinnott, 1963, Frazetta, 1975). Growth is not an irregular process; the various dimensions are closely related.

Though some dimensions grow faster than others the ratio of their exponential rates is constant. Form changes progressively during developement in a constant, correlated fashion. In fact, even relative chemical composition follows this relationship.

These correlated ratios are determined by simple genes. (Sinnott, 1963). In fruit, for instance, there are genes which tend to flatten, elongate or otherwise distort the shape, and they show independent assortment into normal mendelian ratios. Some have even been located on linkage and chromosome maps. Likewise such genes are recognized in drosophila that affect the form of the body, eyes and wings.

Sinnott (p. 101) observes that "Genes show their particulate character as they segregate and recombine, but not as they govern development. Once a genotype has been established it controls the entire living system as a whole."

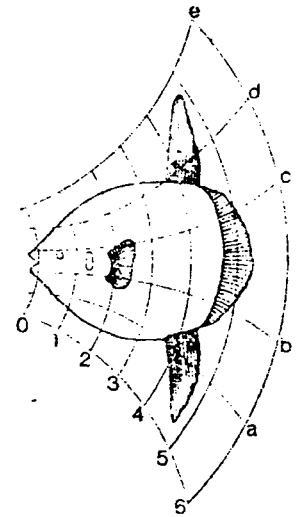
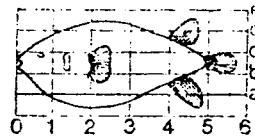
The most striking evidence of the evolutionary significance of developmental correlation comes from d'Arcy Thompson's On Growth and Form (1942). Here he has shown how the shape of one species may be transformed mathematically into that of another, as in figure 6. These shapes have not been arbitrarily re-designed; they have been evenly distorted according to simple equations. Each point retains the same co-ordinates but the grid has been systematically distorted. This is precisely the sort of change that we have seen can be accomplished by single genes. So we again have reason to de-emphasize the significance of random cumulative changes. "This has implications for evolution-

ary theory since a slight change, as by a mutation, will affect many parts of the organism, but their coordination will be preserved. In many cases this unborn correlation assures that a whole gamut of changes will continue to be related to each other since, as aspects of an organic form, they are parts of a continuous whole and are not independent." (Sinnott, p. 41).



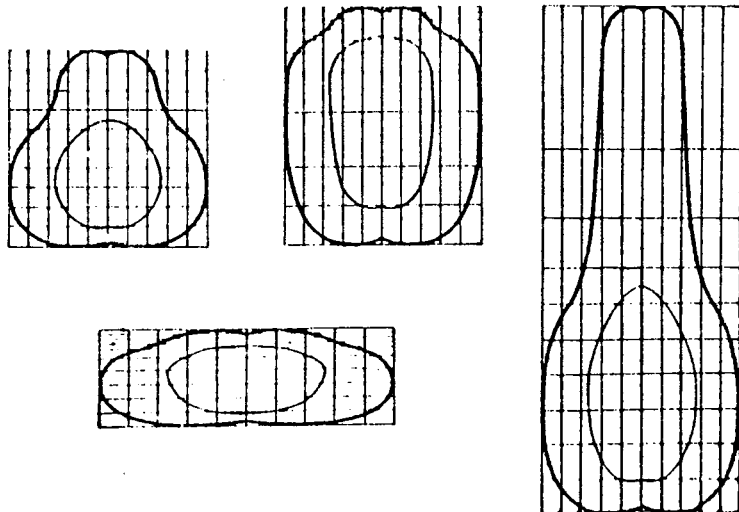
Skulls of baboon, chimpanzee and man (after D'Arcy Thompson)

figure 6a.



Sun fish and porcupine fish (after D'Arcy Thompson)

6b.



Forms of various fruit-shape types inscribed in rectangular coordinates, derived by transformation of the isodiametric type at the upper left.

6c.

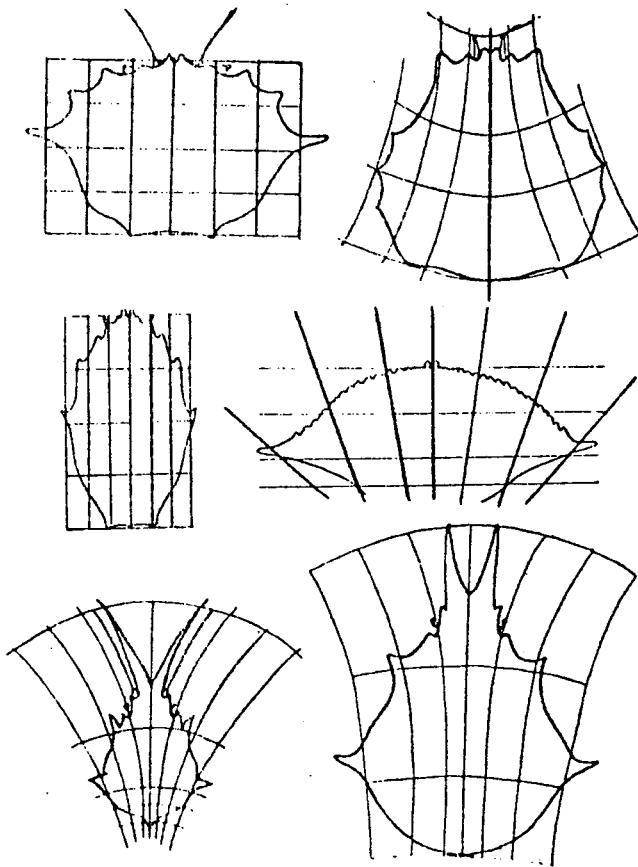


FIG. 13. Carapaces of six genera of crabs inscribed in rectangular coordinates that have been transformed in various ways. Each can be derived from any of the others, in this case from the figure in the upper left. (Thompson, 1942.)

It becomes apparent that the aspects of integration and correlation just discussed provide an organism with a capacity for adjusting itself to the environment and to internal changes in an advantageous manner. I will refer to this ability as "adaptability". Frazetta has another bone example that illustrates this beautifully:

"Throughout life, the periosteal and endosteal sheaths [of the limb bone] remain as a potential source of both osteoblasts and osteoclasts. This permits bones to grow after birth or hatching, and is also the basis for changes in form that can and do occur throughout an individual's life-

time. Perhaps the most fascinating aspect of these changes in form is that they may represent mechanically correct responses to changing environments. A bone is shaped by genetic controlling factors, but also by the patterns of growth of surrounding tissues and by external stresses that act on the bone. Of course, all these factors imply genetic control since, in any final analysis, the genes make bones capable of responding to all these influences.

For any given species there is a "normal" or usual pattern of stresses acting on a bone during ontogeny. These may come from the pullings and bendings of neighboring tissues, the stresses produced by contracting muscles, or the weights and impacts that bones must normally bear. A growing bone removed from its normal surroundings and cultured in isolation attains a general shape very reminiscent of the bone it is supposed to be, but it lacks many structural details that would normally be present. Direct genetic control carries the bone only so far in its developmental progress and then abandons it to the indirect genetic control mediated by external stresses. Without this, the bone is unfinished.....The finishing of a bone's shape is indirect from the genetic standpoint, but direct from a functional standpoint. A bone's shape directly adjusts to surrounding tissues. It is directly fashioned to stresses of muscle pull, to available blood supply, and to individual weight and use of the bone. The joint surfaces can adjust to one another in subtle ways. Thus bones compensate for individual peculiarities: the skeleton is tuned to its surroundings.

In a population of moderately sized animals, the need to possess a system of appropriate responses between weight and limb width can result in a biological organization that "recognizes" and "appreciates" pertinent physical laws." (Page 181-2).

Adaptability could be considered a major adaptation of all animals. Such capacity for adjustment is necessary for the successful "building" of an organism and would thus have high selective value. Such adaptive systems also possess potentialities for modification that to some degree

determines the direction of further evolution. It should be stressed that this can also "tend to promote future evolutionary change itself". (Frazetta 1975, p. 213, emphasis added).

The importance of these non-random aspects of evolutionary change of organic form will become the focus of our attention in interpreting the fossil record. But there is still more to say about adaptability.

It should be made clear that adaptability can only exist by way of the hierarchical nature of developmental strategies. Koestler (1967) discusses at length how it is that complex systems arranged as hierarchies allow flexibility within stability and that, in fact, complex systems do not exist in the universe that are not arranged as hierarchies.

Figure 1 shows hierarchical order, where sub-wholes at each level are composed of those from the next lower level. Koestler has coined the term "holon" for a member of a hierarchy, and I think it is important to show his reasoning:

"The first universal characteristic of hierarchies is the relativity and indeed ambiguity, of the terms 'part' and 'whole' when applied to any of the sub-assemblies. Again it is the very obviousness of this feature which makes us overlook its implications. A 'part', as we generally use the word, means something fragmentary and incomplete, which by itself would have no legitimate existence. On the other hand, a 'whole' is considered as something complete in itself which needs no further explanation. But 'wholes' and 'parts' in this absolute sense just do not exist anywhere, either in the domain of living organisms or of social organisations. What we find are intermediary structures on a series of levels in an ascending order of complexity: sub-wholes which display, according to the way you look at them some of the characteristics commonly attributed to wholes and some of the characteristics commonly attributed to parts. ...The members of a hierarchy, like the Roman god Janus, all have two faces looking

in opposite directions: the face turned towards the subordinate level is that of a self-contained whole; the face turned upward towards the apex, that of a dependent part. One is the face of the master, the other the face of the servant. This "Janus effect" is a fundamental characteristic of sub-wholes in all types of hierarchies.

...It seems preferable to coin a new term to designate these nodes on the heirarchic tree which behave partly as wholes or wholly as parts, according to the way you look at them. The term I would propose is "holon", from the Greek 'holos' = whole, with the suffix 'on' which, as in proton or neutron, suggests a particle or part." (p. 48)

At the base of a hierarchy, the holons show rigid stereotyped and specialized patterns of activity, while those toward the apex are increasingly more flexible; they have at their "command" the results of all the lower levels. The total result - the flexibility and stability of the apical holon - is far more significant than the "sum of its parts".

Examples of biological holons are numerous, for instance the quasi-independent nature of mitochondria and "in vitro" isolation of functioning organs.

Anyone familiar with embryological development should immediately recognize it as a temporal hierarchy. The apex is the fertilized egg and the "branching" follows the progress of time so that the different levels represent successive stages of development. Through each level the holons (i.e. tissues) become progressively less flexible, less "totipotent".

Koestler concludes:

"Genetic atomism is dead. Hereditary stability

and hereditary change are both based, not on a mosaic of genes, but on the action of the gene-complex 'as a whole'. But this face-saving expression - which is now coming into increased use - is empty, like so many other holistic formulations, unless we interpolate between the gene-complex as a whole, and the individual gene, a hierarchy of genetic sub-assemblies - self-regulating holons of heredity, which control the development of organs, and also control their evolutionary modifications...A hierarchy with its built-in, self-regulatory safeguards, is a stable affair. It cannot be pulled in here, pulled out there,.... It is capable of variation and change, but only in co-ordinated ways and only in limited directions." (pp. 134,135)

Thus the transformations shown by D'Arcy, where variation is inter-dependent, would be accomplished by changes at the apex of the hierarchy, which "co-ordinates the pattern of the whole by harmonizing the relative growth rates of the various parts". (Koestler, p. 142).

In essence, if one truly understands the potential of hierarchical organization then it will be recognized that all that has been said here about integration, correlation, and adaptability is tantamount to saying simply "living beings are organized as functional and structural hierarchies". A realization of this should be a significant factor in a new synthetic theory.

From our understanding of the developemental hierarchy it is easy to see that a change at an early stage of developement can have a larger effect on the whole course of developement, and therefore on the final form, than a change at a later stage. DeBeer's book, Embryos and Ancestors (1958) is based on this idea. It is a classic work in exposing the fallacy of the now universally rejected idea that "ontogeny

recapitulates phylogeny". He shows that evolution frequently involves alteration or reversal of developmental sequences (heterochrony) and is not simply the "piling up of new variations at the end of the life history, for the successional order of the pile is not necessarily respected". (DeBeer, 1965, p. 7).

Thus Lovtrup says:

"The important consequence of the view advocated here is that a large phylogenetic change determining, say, the origin of a new taxon of high rank need not arise as a result of a long series of accumulated mutations. If a change, even a slight one, occurs sufficiently early in the sequence of operational steps, it may have very far-reaching effects. Thus, it is not at all necessary, nor even warranted, to presume that a new protein or differentiation pattern is engaged for, as we have seen, the same very limited number of differentiation patterns are involved during the early embryonic stages in widely diverging animal taxa." (p. 102)

DeBeer gives numerous examples where revolutionary revisions have occurred by such heterochrony, illustrating that the degree of change depends not on the degree of genetic change, but at what time in development the alteration first appears. The co-ordination and adaptability of the organic hierarchy can allow such changes to be in harmony with the organism.

The ease by which dramatic alterations can be produced is demonstrated by Lewis (1963). There are five tightly linked genes in *Drosophila* that control the appendages of the thoracic segments. Various mutations of these genes can cause wings to develop in odd locations, including the abdomen, where wings have never existed

in the history of the insect lineage (but appendages have).

Rawles (1963) showed that transplanting chick epidermis to different stages in development could result in the production of scales or feathers in areas which had never had them in bird history.

There is reason to believe that in general characteristics are not lost, but are merely left undeveloped. Thus the loss of toes in horse evolution needn't have been due to an accumulation of small random reductions, but instead may simply have been a cessation of development. In fact, occasional mutants occur among modern horses that have additional toes.

Observations such as this have prompted de Beer (pp. 96 & 97) to note:

"Now, it is often said that the structural changes which take place in evolution are irreversible, and that no case is known in which a race of animals after having lost a character acquires that identical character again. The problem is, however, not quite so simple, for the 'loss' of a character may be due to fairly recent changes in the hereditary factors, changes which may still be reversed, resulting in a reconstitution of the original conditions."

Siamese twins and two-headed cows attest to the malleability of living hierarchies; but there is another aspect of developmental flexibility that results in specific inflexibility of adult form. It has been named developmental canalization by Waddington (1975), and he is its primary investigator.

Frazetta describes it well: (pp. 214-215)

"One type of flexibility has the ironic effect of reducing phenotypic variations among individuals.

The individual deviations in form, which create the variations, could be the result of a number of things gone wrong in the developmental process. A gene mutation, mechanical trauma suffered by the embryo, or unexpected temperature or humidity changes are all potentially capable of twisting the path of development toward an abnormal, possibly inadapative, phenotype. But there is, in many animals, a counter- ing mechanism which can recognize a twisted develop- mental path and which, by appropriate government over further ontogenetic events, can switch the progress of development back toward its normal destination."

From Sinnott (p. 77):

"Development is not necessarily linear. An organism does not advance in its development like a row of standing dominoes, where one knocks over the next until the end is reached, but rather like an open-field runner in football who, if he is not able to go straight toward the goal line, ducks and dodges and avoids the obstacles as well as he can. What gives unity to his behavior is the end toward which he moves, which remains constant despite frequent changes in his course. Many cases are known, both in development and in physiology, where alternative routes may be followed. The organism is thus protected against the disaster that would attend too rigid a procedure."

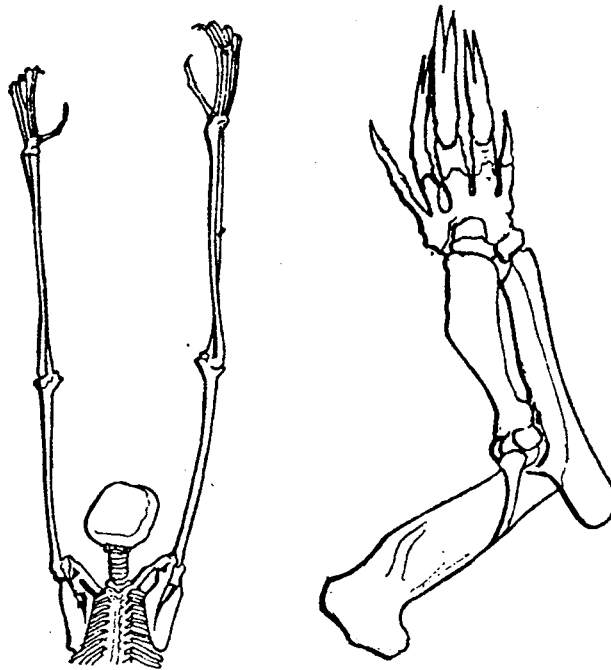
Koestler interprets canalization as a function of the autonomous, self-regulating holons within the growing embryo.

Waddington has demonstrated the selection for canalization in drosophila. Lower sensitivity of eye size to altered larval temperatures was selected for in strains where the size had previously been more proportionally affected by temperature. He also notes that wild type flies are more resistant to changes affecting development than inbred laboratory strains because, in wild populations selection has favoured such genotype combinations.

We must remember that canalization occurs because it is selected for. In the case of an important adaptation (that was independent of environment fluctuations) selection would favor populations with genotypes that would invariably arrive at the optimum type. (This has interesting consequences: how and when can a population break away from this restriction to alter its adaptation? This will be considered in the later section on Selection.)

The result of an organisms's adaptability responding to factors in its adult life is what Waddington calls "exogenous adaptation". "Examples", he says "are legion. If muscles are continually and intensely used, they become thicker and stronger; if one kidney is removed from a mammal, the other hypertrophies; if the forelegs are absent at birth, or removed shortly afterwards, from rats or dogs, the hind-limbs become modified to suit the bipedal gait which the animals are forced to adopt; if skin is subjected to frequent rubbing and pressing, it thickens and becomes more horny; and one could multiply such instances almost indefinitely." (Waddington, p. 25)

There are also adaptations which appear as though they could be due to the same effect but are found to be hereditary. Such "pseudo-exogenous" adaptations are exemplified by the differences in arm structure shown in figure 7, where the two species use their arms quite differently. Waddington contends that the action of canalization and exogenous adaptation together may produce what he calls genetic assimilation, which has the appearance of Lamarkian "inheritance of acquired characters."



The skeleton forelimbs of a gibbon (left) and of a pangolin.

figure 7.

He explains it as follows:

"The occurrence of an adaptive response to an environmental stimulus depends on the selection of a suitable genetically controlled reactivity in the organism. If it is an advantage, as it usually seems to be for developmental mechanisms, that the response should attain an optimum value more or less independently of the intensity of stimulus received by a particular animal, then the reactivity will become canalized, again under the influence of natural selection. Once the developmental path has been canalized, it is to be expected that many different agents, including a number of mutations available in the germplasm of the species, will be able to switch development into it; and the same considerations which render the canalization advantageous will favour the

supersession of the environmental stimulus by a genetic one. By such a series of steps, then, it is possible that an adaptive response can be fixed without waiting for the occurrence of a mutation which, in the original genetic background, mimics the response well enough to enjoy a selective advantage." (Waddington, p. 22)

Waddington has done selection experiments in *Drosophila* that demonstrate the occurrence of genetic assimilation. He points out that what this implies is not that any new genetic principles have been discovered, but rather that "well-accepted principles lead to evolutionary consequences quite other than those which have usually been supposed to follow from them," (p. 92) and that "we can once again find justification for attributing the 'appearance of design', or co-ordinated adaptations, to the epigenetic processes which we know to have co-ordinated effects; and we can reduce our dependence on the abstract principle that natural selection can engender states of high improbability." (p. 56).

Waddington devoted considerable time to the development of the kind of paradigm that would be involved in a new synthetic theory of evolution. He refers to it as a "theory of phenotypes", and recognizes two main elements: 1) "genetic assimilation", an aspect of adaptability that could lead to directed and non-random but gradual evolution; and 2) the theory of 'archetypes' - referring to the modes of change by which the larger phyletic categories (archetypes) could have suddenly arisen, involving other aspects of adaptability and heterochrony.

Armed with this new perspective, let us again look at the fossil record.

INTERPRETATION OF SYSTEMATIC DISCONTINUITY

"The course followed by evolution appears to have been broadly as follows. From a generalised early type, various lines radiate out, exploiting the environment in various ways. Some of these comparatively soon reach a limit to their evolution, at least as regards major alteration. Thereafter they are limited to minor changes such as the formation of new genera and species. Others, on the other hand, are so constructed that they can continue their career, generating new types which are successful in the struggle for existence. The new type repeats the process. It radiates out into a number of lines, each specialising in a particular direction. The great majority of these come up against dead ends and can advance no further: specialisation is one-sided progress, and after a longer or shorter time, reaches a biomechanical limit...." (Huxley 1964)

Figure 8 illustrates this pattern. The cause is generally interpreted in terms of "niche space". (Frazetta). Initially the available niche spaces were filled by an explosive evolution of totally different adaptive types. As these became more established and diverse the occurrence of new types became less frequent and less major, due to the consequently greater partitioning of the environment and narrowing of niche spaces. Nevertheless, new types still occurred sporadically, radiating quickly into specialized lines.

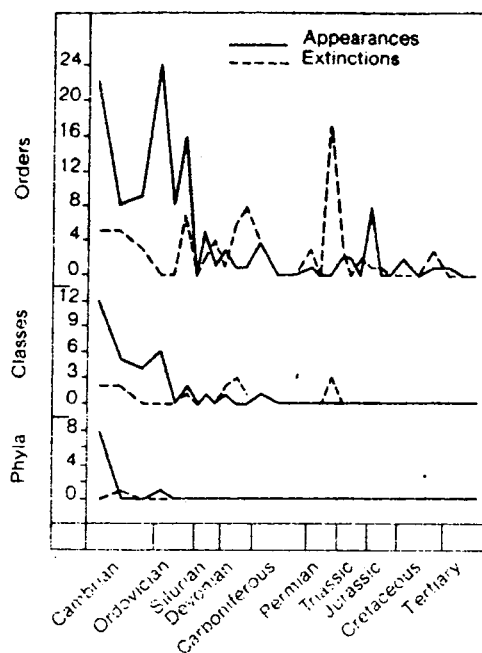


figure 8.

Appearances and extinctions of shallow-water, marine, and benthonic (bottom-dwelling) invertebrates through geological time. (From Valentine, 1969)

Of the new types, the initial transitional forms must have been alterations with "renewed" evolutionary potential, so that "a major factor in large-scale evolution has been this sort of "hitting-the-jackpot". (Waddington, p. 199)

As I have shown, the major problem for Neo-Darwinism is to explain how such transitions were effected gradually; or why, even if they were, they do not appear that way to paleontologists. But "when evolution is considered from an epigenetic point of view, then the problem facing neo-Darwinism is resolved, for most of the systematic differences on all taxonomic levels appear to be all-or-none steps." (Lovtrup, 1974, p. 407)

With the realization of the adaptability of organic form these jumps no longer appear quite so formidable. De Beer(1958)describes the process in terms of two types of change: paedomorphosis and gerontomorphosis. Gerontomorphosis includes modification of adult structures which are already highly specialized. Paedomorphosis includes changes in earlier stages, which are consequently more radical. It encompasses caenogenesis - changes in larval or young stages only; deviation - changes in an early stage retained in the adult; and neoteny - involving retention of larval features while sexually mature, such as the recognized "feotalization of man", so-called because humans exhibit many features distinguishing a foetal ape.

De Beer suggests that paedomorphic changes result in a more generalized and malleable type capable of bursts of adaptive radiation, whereas gerontomorphosis can only carry an already specialized evolutionary line a step further in the same direction.

De Beer gives numerous examples of the different sorts of evolutionary changes (though Lovtrup disagrees on the interpretation of some of them). Figure 9 is his list depicting the degree of change found in known examples of each type of change. (The top three categories are paedomorphosis).

Associated with	The degree of divergence in phylogeny between the following:	Is of the value of a
Caenogenesis	<u>Lineus gesserensis</u> , larval dimorphism	race
	<u>Chironomus salinarius</u> , larval dimorphism	race
	<u>Peripatus capensis</u> and <u>P. balfouri</u>	species
	<u>Polygordius lacteus</u> and <u>P. neapolitanus</u>	species
	<u>Acronycta tridens</u> and <u>A. psi</u>	species
	<u>Culex</u> , <u>Chironomus</u> , and <u>Corethra</u>	genus
	<u>Unio</u> and other Lamellibranchs	family
	<u>Sitaris</u> and other Coleoptera	family
	<u>Haemocera</u> and other Copepoda	family
	Amniota and other Chordata	class
Deviation	<u>Portunio</u> and other Isopoda	family
	<u>Entoconcha</u> and other Gastropoda	family
	Hermit-crab and other Crustacea	family
	Flat-fish and other Telcostei	order
	<u>Antedon</u> and other Echinodermata	order
	Gastropoda and other Mollusca	order
	Monocotyledons and Dicotyledons	sub-class
Neoteny	<u>Amblystoma</u> and axolotl	species
	<u>Polystomum integerrimum</u> and <u>P. ocellatum</u>	species
	<u>Homo</u> and other Primates	family
	Conchostraca and Cladocera	order
	Tetracorallia and Hexacorallia	order
	Appendicularia and other Tunicata	order
	Proparia and other Trilobita	order
	Insecta and Myriapoda	class
	Chordata and Echinodermata	phylum
Adult variation	mutants	race
Hypermorphosis	<u>Gryphaea</u> and <u>Ostrea</u>	genus
Acceleration	<u>Zaphrentis delanovei</u> and <u>Z. parallela</u>	species
	<u>Titanotherium</u> with and without horns	genus
	<u>Cycloclypeus</u> and <u>Heterostegina</u>	genus
	<u>Leptoplastus</u> and <u>Ctenopyge</u>	genus

figure 9.

He notes that "It is probably not without significance that the groups which provide the best examples of recapitulatory effects are the Foraminifera, Lamellibranchiata, and Brachiopoda, which are precisely those which have made the least progress during evolution." (p. 87)

The idea, then, is that "A race may become rejuvenated by pushing the adult stage of its individuals off from the end of their ontogenies, and such a race may then radiate out in all directions...until racial senescence due to gerontomorphosis sets in again." (De Beer, 1958, p. 118)

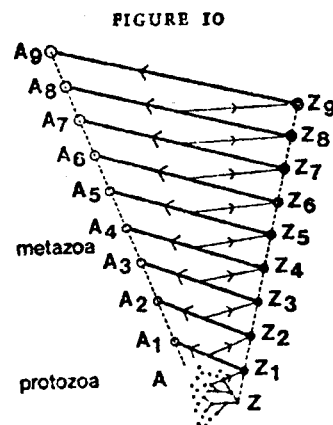


Figure 10 represents the progress of evolution by pedomorphosis. Z to Z₉ represents the sequence of zygotes, and A to A₉ the sequence of adults that result, via ontogenesis (the thick lines), from those zygotes. The thin lines, representing pedomorphosis, branch off from an unfinished stage of one ontogeny to become the start of a new one.

"The essence of the process," says Koestler (1967), "is an evolutionary retreat from specialised adult forms of bodily structure and behaviour, to an earlier or more primitive, but also more plastic and less committed stage - followed by a sudden advance in a new direction. It is as if the

stream of life had momentarily reversed its course, flowing uphill for a while, then opened up a new stream-bed." (p. 167)

According to de Beer, the theory of paedomorphosis "not only explains the gaps in the fossil record, but also supplies the reason why such gaps must be expected." (p. 100) He also suggests that, unfortunately, all the variations studied by geneticists is gerontomorphic. Scudder (unpublished) substantiates this view: that most genetic analysis is on minor variations of adult form, which are not the cause of large scale change.

De Beer calls the potentiality of evolving further evolutionary plasticity. He suggests one aspect of the plasticity created by paedomorphosis is due to the genes "left over" from old adult characteristics that no longer appear in the new form. These "unemployed genes" would be immediately available for further adaptation.

A second aspect is histogenic plasticity, resulting from the fact that the new organization is essentially of tissues from more "embryonic" stages, which are known to be more plastic.

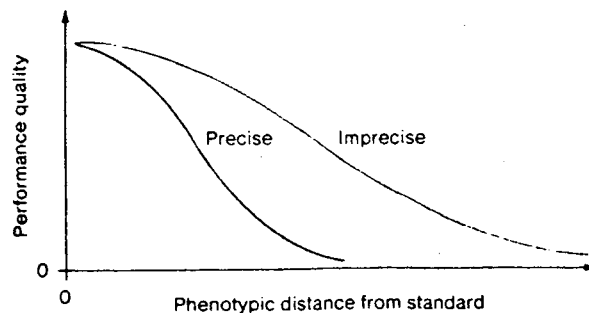
These ideas are questionable.

It would seem that the major basis of the new plasticity is the lesser degree of specialization, for: "The results of gerontomorphosis, on the other hand, are progressive specialization of the adult structure, usually in adaptation to some more or less restricted mode of life. If, then, climatic or other external factors arise or change, upsetting this mode of life, the animal being unable to evolve further will have no alternative to extinction. But primitive animals are not committed

to any particularly restricted mode of life; they are generalized instead of being specialized, and they will be less likely to undergo extinction as a result of environmental change, for they possess plasticity." (de Beer, p. 99.)

We can see now also another reason for the decline in higher taxonomic "jumps" through evolutionary history: "Since the creation of a new grade or phylum must imply modification of the earliest embryonic stages, it seems that the likelihood of such an event would become smaller as the epigenesis of existing animals became more and more complex." (Lovtrup, 1974, p. 864)

The appearance of new archetypal forms is described by Frazetta (1975) in terms of precision. There is much controversy over whether or not organisms are "perfect"; whether every characteristic is at a precise optimum design. Frazetta defines precision by how much a phenotype can be altered before the quality of its "performance" noticeably drops. Precise and imprecise states are illustrated in figure 11.



Relative adaptive precision of two hypothetical systems.

figure 11.

If an organism may be altered such that its performance is improved, then it is relatively imperfect. (There is no absolute sense of perfection involved here). Frazetta then goes on to adapt this idea to Wright's adaptive landscape (1932) but figure 11 will suffice to conceive of it. Higher peaks represent higher performance, and narrower sharper peaks represent greater precision. A wide imprecise peak may nevertheless be higher than a narrow precise one.

Using the evolution of engine design as an analogy to organic evolution, he points out a general trend where an original machine will be made more and more precise, (i.e. ~~the~~^a peak becomes higher and narrower) with a consequent increase in performance, until it can go no further. Later a new, fundamentally different design, with far superior performance, will be invented. At first, however, it will be imprecise, (higher but wider) and will soon be refined to achieve its optimum performance and precision.

We can easily see such a trend in the archetypal jumps and fossil-record gaps. Here, at the earliest manifestation of a new and innovative adaptation, there would be a rapid selection for greater precision. "This speedy voyage through the transitional steps", Frazetta concludes, "has the implication of a relatively short transformation time and, consequently, relatively few intermediate forms. Intermediates are thus, quite simply, harder to find preserved as fossils." (p. 141-142).

Now the question arises, "How sloppy can the initial steps be? The greater the sloppiness that can be suffered, the easier it is for a major change to evolve." (Frazetta, p. 142). I will look into this later.

We have now made a step toward a more concrete interpretation. New archetypal themes have been able to appear suddenly due to paedomorphic-like changes in conjunction with the buffering and directing effects of the adaptability and coordination of the organic hierarchy. They are initially imprecise and radiate to more precise forms; then slowing, by gerontomorphic changes, to "racial senescence", awaiting a new archetypal outburst. In addition, genetic assimilation allows gerontomorphic changes to be much more than strictly random.

"In other words, evolution is neither a free-for-all, nor the execution of a rigidly predetermined computer programme. It could be compared to a musical composition whose possibilities are limited by the rules of harmony and the structure of the diatonic scales - which, however, permit an inexhaustible number of original creations." (Koestler, p. 148.)

The most basic archetypes (those distinguishing phyla) arose just before the beginning of the Cambrian. Such steps were not necessarily "difficult", since, says Lovtrup (p. 451) "The morphogenic preconditions for their establishment are mostly relatively simple epigenetic events...

all of these features are characterized by working in an all-or-none fashion. Therefore, although the effects of the mutations responsible for the transition from one archetype to another may be trivial on the chemical level, they have had a very profound effect upon the epigenetic outcome of the morphogenetic processes."

Indeed, the metazoa may well be totally polyphyletic. (Kerkut, 1960) Even the lower taxonomic archetypal jumps may have occurred with more

"ease", and more frequently, than is normally recognized; for each of fish, amphibia and arthropods are now generally considered by taxonomists to be polyphyletic; no one thinks the mammals are one class anymore (they probably evolved four separate times); and there is at the present time equal evidence for vertebrate descent from any other phylum. (Scudder, unpublished)

"The repeated emphasis of all these arguments is that a relatively meager number of fundamental patterns underlie a great animal diversity....Within broad groupings of animals the apparent array of greatly differing forms might in a sense be misleading. Differences are there, but their evolutionary distinctness in pattern and program is possibly less than our esthetic perceptions easily allow. The greatest feat of the evolutionary process might lie in its having completed its great feats. In this accomplishment it has done almost all that could be done for the creatures of the past, and, inadvertently, for those to come later in whatever world the future designed." (Frazetta, p. 237)

What we have considered so far implies several things:

- 1) that the fundamental steps in evolution may have been the contribution of individuals rather than populations;
- 2) that the initial stages in these transformations were relatively imprecise; and
- 3) that we need revised ecological considerations regarding the survival of new forms in new niches. I will now consider these problems.

SELECTION

According to Mayr (1967) most selection "maintains" a population at a static position in its adaptive zone. In the cases of selection for change, Simpson (1944) and Mayr (1967) recognize three categories:

1) Speciation, involving subzonal specialization of sub populations. The change is minor and slow and leads to the formation of new sub-species, species or genera.

2) Progressive (Mayr) or phyletic (Simpson) evolution, involving large isolated populations whose adaptive zones are changing. It leads to moderate change, up to the genus or family level, by accumulation of minor adaptive alterations.

3) Quantum (Simoson) or Switch (Mayr) evolution, occurring when small populations "switch" to a new adaptive zone. The change is radical and rapid, leading to the origination of taxa from families to phyla.

Simpson (1944), Mayr (1967) and Dobzhansky (1970) give examples where huge differences in evolutionary rates are known. One species may remain unchanged for 900 million years, whereas another may show dramatic transformation in 100 years. It is the fast rates that we have been considering. They involve switch evolution, and occur in small populations.

Mayr is one of the leading neo-Darwinists, yet he makes it clear that large populations, which population genetics is based on, are not going anywhere. A successful species, he says:

"...can spread widely, become very populous, and can continue to improve slightly by progressive evolution. But once it reaches its adaptive peak, it will be subject primarily to maintenance

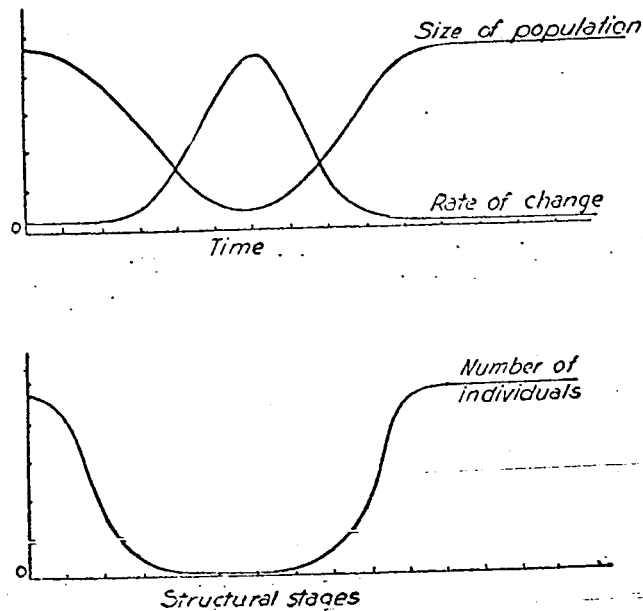
evolution. When a species reaches the status of a successful widespread populous species, it seems that it becomes rather incapable of undertaking major switches or acquiring major evolutionary novelties. It is also unable to speciate, at least within the main body of the species.

I might say the widespread populous species is what the paleontologist usually finds in a fossil deposit simply as a matter of chance. Much of evolutionary theory that we have learned from paleontology is quite true for widespread populous species but this doesn't give us a complete picture of evolution. In fact, it has in a way almost falsified the picture." (1967, p. 52)

The reason for this restriction on large populations is due to canalization: "The longer a genotype is maintained in evolution, the stronger will its developmental homeostasis, its canalizations, its system of internal feedbacks, become. The stronger such an internal cohesion is, the more the genotype will respond to selection pressures as a whole rather than as an aggregate of individual genes....As soon as one adopts the model of the internally balanced, almost totally homeostatic genotype, one can justify evolutionary constancy in the presence of normal mutation and selection rates." (Mayr, p. 53)

One of the puzzles of evolution, then, is how to break up such a canalized system without causing extinction. This can occur only in small populations, where "The canalization and the homeostatic mechanisms seem to break down owing to increased or extreme homozygosis: and the changes in the phenotype that happen under these circumstances give selection a new handle by which it can do things that it cannot do in large gene pools." (Mayr, p. 50)

Simpson (1944) illustrates this idea in the form of a graph given in figure 12.



—Reduction of number of individuals demonstrating major structural changes. In such sequences increased rate of evolution coincides with decreased size of population (upper figure). There are, then, more distinguishable structural stages per unit of time and also fewer individuals per unit of time than in the normal evolution of large populations. The result (lower figure) is an extreme and long-continued reduction in the number of individuals exemplifying each structural stage.

figure 12.

Another factor is suggested by the work of Thompson (1976), who has done experiments to indicate that sexual recombination itself may be, contrary to orthodox interpretation, a conservative force; and it is recognized that small populations lose the "benefit" of sexual recombination.

Lovtrup (1974) emphasizes the necessity of isolation for the survival of new types in switch evolution. "Isolation may..., through

the elimination of interspecific competition, ensure the progression and survival of a population of individuals characterized by the possession of properties differing from those of the population from which they stem." (p. 428)

He recognizes two types of isolation, random and non-random. Non-random isolation obtains in those situations where an organism with a new adaptation arises that is "pre-adapted" to a new niche, in which it must immediately become isolated for its success. Random isolation is more relevant for our attention. "Random isolation may involve isolation before mutation but also isolation of a mutation. From a classical neo-Darwinian point of view this makes no great difference, but if more than small mutations are allowed for, then the possibility obtains that a mutant, embodying a disadvantageous gene, may progress and survive in isolation, being exempt from both intra- and interspecific competition initially, and from the latter kind later on when the new niche is sated." (Lovtrup, p. 429, 430)

Another reason for isolation is given by Mayr, where "If you are in the process of switching into a new adaptive zone you are (if I may use such anthropomorphic language), painfully building up the new gene complex that adapts for this new situation. To have it polluted all the time by genes from the parental gene pool pulls you back again to where you started from." (1967, p. 50)

Lovtrup's random isolation appears as the "baldwin effect" (Frazetta), diagrammed in figure 13.

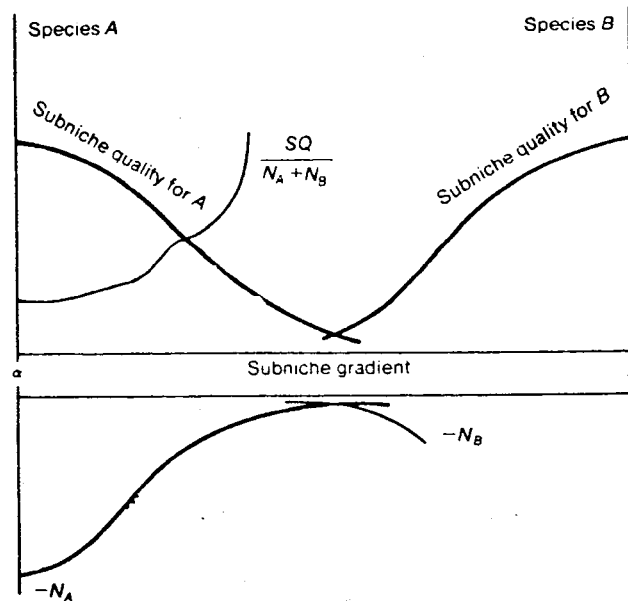


Figure 13.

The upper curves show subniche quality for two species in respect to a gradient. The lower curves show the number of individuals, which decreases with quality. The ratio of subniche quality to the number of competing individuals, however, markedly increases towards the boundary of the species' dispersal range. Our new, hypothetically imprecise organisms would here gain an advantage by occupying this essentially empty subniche (while greater precision was being selected for.).

Lovtrup points to the situations of Neopilina and Latimeria as examples.

"Clearly, evolution has long ago bypassed the level represented by these animals, and if they had not managed to escape interspecific competition by seeking refuge in the depths of the sea they would surely have suffered the fate of their congeners, extinction. These examples, as well as the history of Marsupialia in Australia and in the Americas, respectively, may serve to illustrate the importance of random isolation for the survival of less 'competitive successful' animals. Similar instances are known from the vegetal kingdom." (p. 431)

In our scheme, if the less "competetive successful" organism were so because of its new generalized, imprecise, but more plastic arrangement,

then it would proceed to radiate quickly into successful specialized lines.

This goes against the grain of established theory, for "the survival of anything but the best is unacceptable to orthodox neo-Darwinism."

(Lovtrup, 1974, p. 430.) This stance is based essentially on Darwin's first two postulates: that ^aspecies overproduces ^{offspring} but remains more or less constant ^{in number}, therefore competing for survival.

But:

"When would a population be least subject to restrictions on its multiplication? When might most of those born survive to reproduce? The answer can only be: when the population is relatively small and occupies a new ecological niche, previously empty; that is, when a small number of individuals of a basically new type are present. These conditions are best met when a major genotypic change is occurring which leads, say, to a new phylum, order, or class...

"Adaptive superiority" is empty of all meaning when an entirely new form emerges and occupies a new adaptive zone, for there is then no competition and no basis for a comparison. It is difficult to avoid the conclusion that the nearer the origin of an entirely new type and the smaller the numbers present, the less important is external selection."
(Whyte, 1965, pp. 66, 67)

Perhaps we must change our paradigms to incorporate the idea that, to quote Fraser (1967, p. 107): "A major feature in understanding the evolution of adaptive form and function is the realization that this is essentially based on the survival of the least inadequate. A successful species is not one which is adapted to a particular environment but rather one which is least badly adapted to that environment. Evolution is based, not on superlatives, but on adequacies."

We can now see with more ease how the principles of adaptability, integration and correlation inherent in organisms can come to the fore during archetypal changes. Whyte (1965) describes this by saying that in such instances "internal selection" is the main directive force in evolution.

He depicts internal selection mainly as a restrictive faculty of an organism's integrative capacities, where "only those changes which result in a mutated system that satisfies certain stringent physical, chemical, and functional conditions will be able to survive the complex chromosomal, nuclear, and cellular activities involved in the processes of cell division, growth, and function," (p. 50), so that "The mutations whose consequences reach the Darwinian test are not necessarily random in relation to phylogeny for they have already been sifted by an internal selection process." (p. 52), and therefore "The conditions of biological organization restrict to a finite discrete spectrum the possible avenues of evolutionary change from a given starting point. The nature of life limits its variation and is one factor directing phylogeny." (p. 53).

He has recognized as well, however, that internal selection "may in special situations go beyond the passive selection of given variations, and by the reformation of inappropriate disturbed genotypes exert a direct molding influence guiding evolutionary change along certain avenues." (p. 70).

Koestler illucidates this further: "We might say that the monkey works at a typewriter which the manufacturers have programmed to print only syllables which exist in our language, but not nonsense syllables.

If a nonsense syllable occurs, the machine will automatically erase it. To pursue the metaphor we would have to populate the higher levels of the hierarchy with proof-readers and then editors, whose task is no longer elimination, but correction, self-repair and co-ordination." (1967, p. 133.)

At times of evolutionary revolutions, then, when a few founders of a new type are isolated in a non-competitive situation "Internal selection would here, in a certain degree, directly determine the variations resulting in phylogeny (provided they pass the Darwinian test), rather than merely select from given biologically arbitrary variations. Here internal selection becomes internal determination, and phylogeny the direct result of internal factors." (Whyte 1965, p. 79) In Whyte's diagram, figure 14, this is the case represented by the far left arrow:

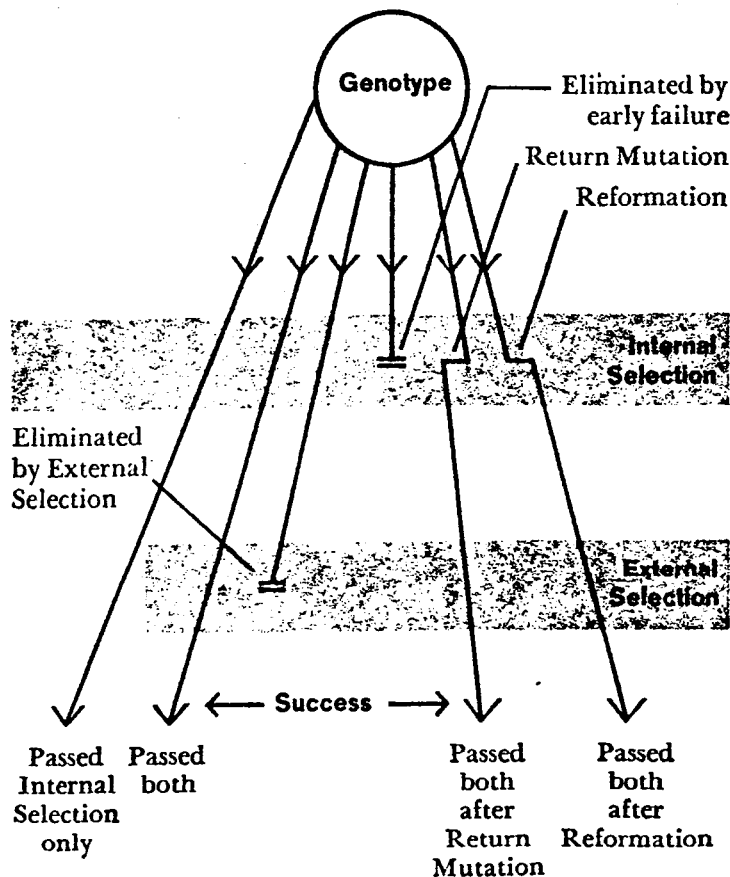


figure 14.

Dodson (1975) has analysed switch evolution by "catastrophe theory". Catastrophe theory is a method derived from topology that has recently been developed by René Thom (1972) to explain phenomena where change is not smooth and continuous. Dodson has shown that if switch evolution occurs it must operate in the form of one particular catastrophe - the "fold catastrophe", and that knowing this provides a way, in principle, of testing whether switch evolution is occurring. Zeeman (1976) explains the theory non-mathematically.

Before going on to a few other considerations, I would like to call to attention again the fact that the developmental adaptability of living beings may allow another non-random method of evolution besides that of archetypal jumps: that of genetic assimilation. This may be an important factor that can occur gradually and without the need of isolation or small populations.

FURTHER ASPECTS OF SELECTION

1. Random drift

In Simpson's description of switch evolution one can recognize that it is a classic case of "founder" or "bottleneck" effect: "The new types are rare while they are developing, which is more likely but not necessarily true in times of great environmental change, and they spread rapidly after they have achieved a new level of relative stability

and their evolution has slowed down and become one of progressive diversification within the now-conquered major ecological zone." (1944, p.115.)

Nowhere would genetic drift be more significant. It may thus be an important factor in evolution.

Neo-Darwinism does not deal with such situations; it requires large panmictic populations. Wright (1948, 1949) has estimated that genetic drift will be in effect in any population of less than 1000 individuals. If we look at wild populations we find that they are often small. The entire population of the small Asian rhinoceros is roughly fifty individuals; the white rhinoceros is two hundred; all tigers amount to 600; there are much less than 1000 wild sheep in North America; and the largest population of black bears in Montana is 84 individuals.

(Scudder, lecture notes)

As well, large populations are usually not panmictic, but composed of small reproductively isolated demes. Even free mixing does not equate to gene-flow, for it depends on the organism's breeding range.

(Eaton, 1970)

Many examples of drift occurring in drosophila and humans have been recorded. (Dobzhansky, 1970). The north elephant seal shows a total lack of protein polymorphism, as a result of a bottleneck effect caused by over-hunting; the Dunkers show unique blood group frequencies indicative of a founder effect; and a group of small Italian villages have been found to show unmistakable genetic drift. (Scudder, lecture notes)

Let us not dismiss the possible significance of random genetic drift.

2. Imperfection and adaptively neutral characteristics

The idea proposed in this paper is dependant on the idea that natural selection involves "survival of the least inadequate". It is generally assumed, however, that all characteristics must be perfect adaptations, and that if we cannot see the functional significance of a characteristic it is due to our own abysmal ignorance. (Arthur Cain, 1964) If this is true it gives my proposition a bad knock. The idea suggests itself by way of countless exquisitely adapted and precise characteristics of organisms throughout the living world. The following example from Frazetta (1975, p. 126) should suffice to illustrate this:

"For years it seems to have been tacitly assumed that the precise abdominal bristle patterns seen in the many *Drosophila* species had no direct adaptive value. But careful observations showed that deviations from the normal bristle pattern, as could be studied in mutant flies, were adaptively unfortunate. Flies with too few bristles were prone to sink into soft, mushy substrates and become helplessly trapped, while mutant flies with too many would often draw beads of water from the same kinds of substrates, which would weigh them down and interfere with normal locomotion (Muller, 1950). Hence even a feature as apparently trivial as the body bristles of fruit flies are precisely organized in a directly adaptive manner."

The evolution of reproductive isolating characteristics at sympatric regions of newly overlapping sub-populations also implies that the "slight" differences are significant enough to select against hybridization.

But we need not accept that all characteristics are perfect. To quote Frazetta again (p. 127): "If a portion of the skeleton is reduced in one species, its adaptive significance is the reduction

of body weight; but if it is enlarged, it adds mechanical strength. This kind of simple approach leads us nowhere. It provides the means to gloss over some real problems on the slippery article of faith that whatever we observe must be adaptively perfect."

One can find instances that also suggest adaptively imperfect or neutral characteristics, such as the survival of severely injured animals in the wild, and sudden population flushes of animals introduced by man into totally foreign environments.

Sinnott (1963) discusses the diverse forms of radiolarians, where, though they occur all over the world, no local predominance of any one type is ever found:

"These tiny skeletons are of the utmost delicacy and complexity, reminding one, in their diversity, of snow crystals. Attempts have been made to find some adaptive significance in these differences which would account for their origin through a selective process. This is very difficult to do, and the suspicion may be justified that in attributing their origin to natural selection we have sacrificed common sense to the requirements of a theory. The innumerable and complex differences among these minute organisms, and among many others, such as the diatoms, with their beautifully marked shells, seem not to be primarily the result of selective advantage but rather to owe their origin directly to molecular forces not unlike those governing the formation of crystals. It is not necessary to invoke natural selection in order to explain the almost infinite variety of snowflakes." (p. 185).

Dobzhansky (1970) and Frazetta (1975) discuss how many useless structures may exist as pleiotropic effects of some overall adaptive characteristic.

The polymorphism controversy comes into play here as well. (Dobzhansky 1970, Lewontin 1974, Clarke 1975, Wills 1970). There is

widespread existence of stable heterogeneity within populations, and it is shown to have a genetic basis. The "selectionists" argue for various selective factors, such as heterozygote advantage and frequency dependent and disruptive selection. Dobzhansky has demonstrated heterozygote advantage in the laboratory, and seasonal fluctuation in the field, of inversion heterozygotes in *Drosophila*.

The "neutralists" suggest that much of this polymorphism is simply adaptively neutral.

Much of the controversy is based on protein polymorphism found by electrophoretic mobility studies and heat denaturation, (Lewontin, 1974), and it is certainly debatable whether all the various iso-enzymes are precisely selected for.

The "variable amino acids" in cytochrome c and haemoglobin of various animals have been used as "clocks" to indicate the "evolutionary distance" of different animals, based on the idea that they changed randomly at normal mutation rates.

We must remember, to quote King & Jukes (1969), that "Natural Selection is the editor, rather than the composer, of the genetic message. One thing the editor does not do is remove changes which it is unable to perceive."

It is not unreasonable to conclude that although many characteristics are precisely selected for, some may be imprecise or neutral. This, then, lends strength to the credibility of the ideas set forth in this paper.

3. The exploitive system

Waddington has shown that the mutation process is not random or independent of the genotype. He also points out that the process of natural selection itself is seen to be partly influenced by the nature of the phenotypes submitted to it when we come to consider that an animal may be choosing a particular part of its heterogeneous environment. Thus the stresses to which it is subjected depend to some degree on its own behavior. These stresses will then further influence its phenotypic expression so that a complex feedback system is involved.

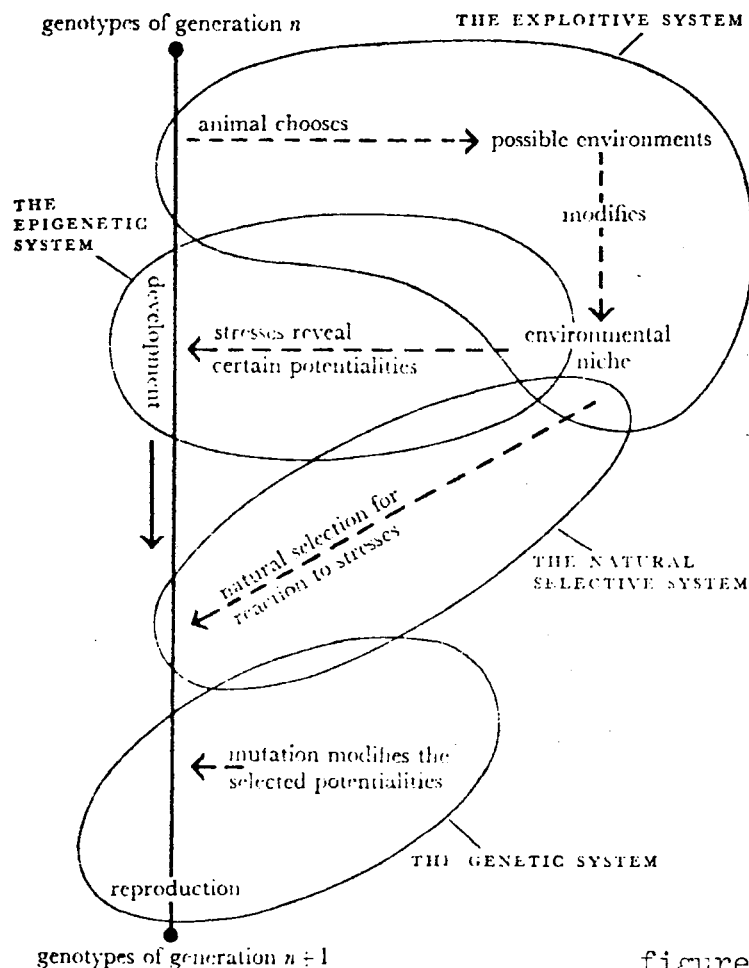


figure 14.

Waddington has demonstrated preferential environmental selection correlated with particular genotypes of *Drosophila*.

According to Waddington, when this factor is incorporated into the evolutionary system the complete picture is as in figure 14. He recognizes four sub-systems: the exploitive, the epigenetic, the natural selection, and the genetic. These must all be taken into account for a sufficient mathematical theory. Lewontin(1974) and Waddington (1975) have elaborated the mathematical and operational problems involved.

4. Speciation

The standard idea is that speciation occurs almost entirely (aside from plant allopolyploidy) by gradual allopatric processes. It would seem no problem, then, to have a "biological species" definition, based on gene flow. But as more is being studied it becomes increasingly plain that this definition breaks down in situations where gene flow is not straightforward, or altogether irrelevant, such as with fossils or asexuals..

Such problems have prompted Scudder (1974) to propose: "it would be preferable to recognize and indeed stress that not all species are of the same kind. Different sorts of species should be recognized and understood in relation to different inherent characteristics and different strategies of evolution. We should thus recognize palaeo-species, morphospecies, sibling species, ring species, polytypic species, biospecies, introgressed species, hybrid species, compilo-species, agamospecies, gynogenetic species, and so on. It ought to

be possible to devise a scheme for designating these and handling them then in a systematic manner."

He suggests in addition that we must realize that gradual allopatric speciation is not the only mode of evolution. There is evidence for "gradual sympatric" speciation by disruptive selection (Waddington 1975, Thoday, 1972.) There is also evidence for "quantum speciation" (such as in Hawaiian *Drosophila* species where divergence has obtained due to founder effects, (Carson 1970, 1971) and "instant speciation" (Carter 1960) where a sudden mutation reproductively isolates an individual from its population. These last two possibilities are important to the previous discussion of sudden switch evolution in small isolated populations.

CONCLUSION

Evolution has involved not only selection for adaptations, but also for adaptability. The latter then results in the non-random appearance of the former; including systematic "leaps".

Thus a theory built mainly on genetics is insufficient; epigenetics must also be considered. This done, we should find that, to quote Lovtrup (1974, p. 412): "...the supreme creative forces of the synthetic theory, intraspecific selection and environmental pressure, assume a much more modest, if not unimportant, role in the drama of phylogenetic evolution. Rather, the real creative agent becomes the mutations responsible for innovations, particularly through interaction with epigenesis, aptly assisted by isolation". Fitness becomes com-

parative; organisms need not be perfect.

One can understand why it is that the Neo-Darwinists disregard the obvious problems and dogmatically assert their theory as sufficient: to admit an epigenetic view means to admit that their theory is a relatively insignificant part of the overall evolutionary process.

But their attitude pervades what is taught in schools, and results in students being brought up in somewhat of a "mental straight-jacket". In a large part this is also the fault of the student himself and the education system. Kerkut (1960, p.3) elucidates this frankly:

"...the serious undergraduate of the previous centuries was brought up on a theological diet from which he would learn to have faith and to quote authorities when he was in doubt. Intelligent understanding was the last thing required. The undergraduate of today is just as bad; he is still the same opinion-swallowing grub. He will gladly devour opinions and views that he does not properly understand in the hope that he may later regurgitate them during one of his examinations. Regardless of his subject, be it Engineering, Physics, English or Biology, he will have faith in theories that he only dimly follows and will call upon various authorities to support what he does not understand. In this he differs not one bit from the irrational theology student of the bygone age who would mumble his dogma and hurry through his studies in order to reach the peace and plenty of the comfortable living in the world outside. But what is worse, the present-day student claims to be different from his predecessor in that he thinks scientifically and despises dogma, and when challenged he says in defence, "After all, one has to accept something, or else it takes a very long time to get anywhere."

The educational system must make an effort to stop fostering such attitudes, and begin encouraging critical questioning and real understanding of subjects - in this case, evolutionary mechanisms.

We have still a long way to go towards a sufficient Synthetic Theory. This paper has not really given any answers, but it has pointed out where the new paradigm-shift lies and what course we must now take to arrive at a complete Synthetic Theory of Evolution.

APPENDIX I - THE PHYSICAL BASIS OF FORM

Sinnot (1963) points out that an understanding of ontological change may require an understanding of the physical factors of which form is a manifestation. He suggests several aspects to study. The paracrystalline nature of much of the protoplasm, for instance, may be a primary step in an orderly pattern that underlies form. Similarly, bio-electric fields (which are known to form precise patterns that slowly change as development proceeds) or concentration gradients, or equilibrium states (due to the position of cells with respect to specific patterns of electron bonds in proteins at their surfaces) may all be important to varying degrees in shaping processes.

Sinnott recognizes three basic tendencies that result from whatever the relevant physical factors may be.

"These three qualities, then - polarity, symmetry, and spirality - seem to be characteristic, to a greater or lesser degree, of the living stuff of all organisms. It is reasonable to regard them as qualities that have existed from the beginning of life rather than having been developed during the course of its evolution. They are found in lifeless as well as in living nature and are not distinctively organic. Their occurrence in organisms may therefore be looked upon as the persistence there of qualities present also in the inorganic world.

The significance of these qualities for the problems we have been discussing lies in the fact that they provide the physical basis for the development of orderly, three-dimensional organic form; the stuff, so to speak, of which form is made. They are general qualities and tendencies rather than specific ones. The specificity of form is provided by the genes, working through the cytoplasm and modified in their effects by factors in the environment. Just how this is accomplished is by no means clear, but I believe that if we are to solve the problem of form it must be attacked through an understanding not only of its genetic basis but of these universal qualities that underlie it." (Sinnott, 1963, pp. 164-165.)

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